Movement of the Cape dwarf chameleon (*Bradypodion pumilum*): are they vulnerable to habitat fragmentation?

Alexander Douglas Rebelo

(arebelo23@gmail.com)
Department of Biological Sciences, University of Cape Town
Rondebosch, 7700
South Africa

Thesis contributes to fulfilment of B.Sc. Honours year

Supervisors: Krystal A. Tolley[1]
Res Altwegg[2]

1. South African National Biodiversity Institute
2. University of Cape Town, Statistics Department

PLAGIARISM DECLARATION

1. I know that plagiarism is wrong. Plagiarism is to use another's work and pretend that it is one's own.

2. Each contribution to, and quotation in, this thesis from the work(s) of other people has been attributed, and has been cited and referenced.

3. This thesis is my own work.

4. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work.

5. I acknowledge that copying someone else's assignment or essay, or part of it, is wrong, and declare that this is my own work.

Signed by candidate

Alexander Douglas Rebelo

Movement of the Cape dwarf chameleon (*Bradypodion pumilum*): are they vulnerable to habitat fragmentation?

Alexander Douglas Rebelo

ABSTRACT

Habitat fragmentation threatens the persistence of natural populations globally. Dispersal between populations can mitigate the negative impacts of habitat fragmentation. The Cape dwarf chameleon (*Bradypodion pumilum*) occupies heavily fragmented habitat and yet few studies have investigated their ability to disperse and thus persist. In this study I monitored chameleon movements and habitat use in the semi-transformed Noordhoek Wetlands, South Africa. Radio-telemetry was used to track adult chameleons (N=11) over 10 days during March 2010 and April 2014. Data were analysed using linear mixed effects models including relevant predictor variables. The chameleon habitat use, such as perch height, thickness and vegetation cover, including their GPS positions, was recorded hourly during the day. The increase in area used by chameleons over time increased at a relatively constant rate. Male and females showed similar areas of utilisation and daily displacement. However, males perched in higher, in less dense vegetation and on relatively thicker stems than females, although the latter two were not statistically supported. Additionally, chameleon vegetation use varied between day and night, but not between early morning, midday and late afternoon, where chameleons perched in higher and less dense vegetation at night than during the day. Habitats surrounded by wide spaces devoid of vegetation could isolate populations of Cape dwarf chameleons. However, the chameleon movement is unhindered by constraints of territory and by connecting habitat fragments together with corridors of suitable vegetation, the effects of fragmentation could be mitigated.

ACKNOWLEDGEMENTS

I sincerely thank my two supervisors, Krystal Tolley and Res Altwegg, Krystal provided the project idea and aided in fieldwork, admin and through the South African National Biodiversity Institute has provided radio-transmitters and access to other equipment. Res has helped with the experimental design and spared invaluable advice on data analysis. Thanks to Leighan Mossop and Jaclyn Smith at SANParks for granting me access to the site. I am extremely grateful to the Nation Research Foundation (NRF) for funding my honours year. I would like to thank Eric Katz for providing access to radio-tracking data collected for his M.Sc. Finally, I am grateful to Pat, Tony and Janet Rebelo for reading on commenting on drafts. This study was done under the SAN-Parks permit "*Investigating the biodiversity, gene flow and dispersal capabilities of amphibians and reptiles in the Agulhas and Table Mountain National Park*". The study was approved by the ethics committee of the University of Cape Town (protocol number: 2014/V4/RA) and the South African National Biodiversity Institute (number: 001/2014).

TABLE OF CONTENTS

INTRODUCTION

All around the world natural habitats continue to be transformed by human activities (Vitousek, 1997). We are currently in a period referred to as the sixth mass extinction (Barnosky *et al.*, 2011), with habitat destruction ranking as the greatest threat to biodiversity (Wilcove *et al.*, 1988). Habitat destruction reduces habitat availability and also affects the functioning of nearby untransformed ecosystems (Saunders, Hobbs & Margules, 1991). Anthropogenic land transformation often progresses in a patchy fashion, enclosing the remaining natural areas within a matrix of transformed habitat, a process called habitat fragmentation. For example, deforestation of the Brazilian Atlantic forests has transformed the once continuous forest into a number of smaller remnant fragments (Brown & Brown, 1992). Conservation has only recently become a global priority, such that many protected areas are only small fragments surrounded and isolated from other protected areas by a transformed landscape.

The fragmentation of once large and continuous habitats into smaller remnants can result in population phenomena that reduce biodiversity. Because many species are specially adapted to their natural environment, they are unable to persist within a transformed habitat. Furthermore, the transformed matrix may impose a barrier or restriction to movement, causing isolation of populations within fragments. The result is a large number of small, isolated populations that are more susceptible to local extinction. For example, the large predators are absent from small Brazilian forest fragments, but persist within the larger fragments (Chiarello, 1999). Populations isolated within small areas are more susceptible to local extinction because a large proportion of their population can be killed by localised disturbances or disasters, such as flooding, fire or volcanism (Shaffer, 1981). Furthermore, their isolation prevents repopulation of individuals from unaffected areas, decreasing the population's ability to recover (Huxel & Hastings, 1999). The isolation of populations is of increasing concern as anthropogenic climate change continues to drive up temperatures over many species' thresholds with fragmentation trapping populations within unsuitable environments (Mantyka-Pringle et al. 2012). The latter are, however, indirect consequences of habitat fragmentation on biodiversity.

Small populations may decline owing to factors that require individuals that number greater than the minimum viable population (Courchamp, Clutton-Brock & Grenfell, 1999). Such factors include genetic diversity, demographic stochasticity and group strategies (Courchamp, Clutton-Brock & Grenfell, 1999). Gene-flow within a population maintains genetic diversity, which prevents build-up of disadvantageous alleles through inbreeding. This genetic diversity increases the population's ability to adapt and survive environmental stochasticity, such as pathogen outbreaks and predation (Keller & Waller, 2002; Reed & Frankham, 2003). Thus isolated populations could be too small to maintain genetic variation, causing reduced fitness and vulnerability to environmental stochasticity. Small populations are also more susceptible to demographic stochasticity, such as skewed sex-ratios. For example, predation or disease could wipe out a large proportion of one sex within a small population by chance, crippling that population's ability to

reproduce. Certain behaviour can also depend on group size, for example, mortality was higher in small groups compared with large groups of suricates, where they rely on vigilance to avoid predation (Clutton-Brock *et al.*, 1999). Populations occupying smaller fragments thus have a higher risk of extinction, which increases with the time since isolation, impenetrability between fragments and matrix degradation (Saunders, Hobbs & Margules, 1991). Thus the vulnerability of a species depends on the landscape changes within its habitat and its ability to cross the transformed matrix between fragments.

The dispersal of individuals between fragments can maintain genetic variation, recover declining populations and act as a buffer against stochastic effects. Dispersing individuals can transfer genetic information from one group to another, preventing localised inbreeding and genetic deterioration. Bohrer et al. (2005) found that persisting, fragmented populations, simulated with long distance dispersal, retained more genetic diversity and had a lower risk of extinction. Dispersal has been shown to reduce inbreeding in many animals, although the causal mechanism remains controversial (Moore & Ali, 1984; Pusey & Wolf, 1996). Populations can be supplemented by dispersing individuals from neighbouring areas (Brown & Kodric-Brown, 1977), replenishing small populations following demographic or environmental stochasticity. However, reckless dispersal across dangerous environments, such as transformed habitats and structures (e.g. motorways), could sabotage a population's survival, (Carr & Fahrig, 2001). Furthermore, some species are naturally poor dispersers and occur in small, isolated populations (Funk *et al.*, 2005). These species can survive under these conditions and should be robust to the effects of habitat fragmentation. Nevertheless, movement between habitat fragments can mitigate the effects of habitat fragmentation and should be investigated to assess risk of local extinction.

The ability of an organism to disperse, and thus escape the constraints of a fragmented habitat, is influenced by intrinsic properties, such as morphology. For example, lizards have developed a large morphological diversity that reflects their use of a vast variety of environments and substrates. Different modes (e.g. climbing and level running) and attributes (e.g. endurance or acceleration) of lizard locomotion are determined by their limb morphology, introducing inherent mechanical trade-offs between these different modes and attributes (Aerts *et al.*, 2000). Thus the lizard limb morphology may hinder movement across unsuitable substrates, such as the transformed matrix between fragmented lizard populations. Allometric factors are also important to consider, as larger animals require more resources and are generally associated with larger home-ranges (Mace & Harvey, 1983), and thus disperse further. Likewise, sparse resource will require animals to move further to consume adequate quantities. However, locomotion is costly. Moving further requires more energy to be used, reducing the resources available for reproduction, and may increase the risk of predation. Yoder (2004) found that predation of Ruffed grouse increased with dispersal distance and also in unfamiliar terrain. This suggests that staying near known refugia, in this case bushes, decreases the risk of predation.

Habitat preferences can be influenced by extrinsic factors, such as predation or interactions between conspecifics and thus may restrict dispersal along such habitats. Interactions between individuals of a species and among species can influence the habitat preferences and thus dispersal ability of some species. Natural predator-prey relationships have a long evolutionary history in which the prey has adapted ways to minimise predation risk. The trade-off between food abundance and predation risk can determine where an organism chooses to forage, and may depend on its life-history (Abrahams & Dill, 1989). For example, slow rodent species remained under the protective cover of bushes, while the least vulnerable species foraged out in the open (Kotler, 1984). Similarly, a species of North American skink more frequently ate crickets placed closer to refuge than those placed further away and thus minimised risk of predation (Cooper, 2000). In fragmented landscapes, the transformed matrix may be devoid of cover and refugia, exposing animals to mobile and aerial predators. The lack of suitable cover and escape routes are likely to hamper the dispersal across the matrix, especially if the fragments are far apart.

Resource and habitat partitioning between individuals also have the potential to influence the overall dispersal ability of a species. Some species have evolved enhanced sexual dimorphism and sex-biased life-histories, as a result of the different reproductive costs between males and females (Trivers, 1972; Emlen & Oring, 1977). For example, many bird species have brightly coloured male birds and duller, more camouflaged females. Males have a higher risk of predation than the females because they are more visible to predators. Males have evolved this strategy because vivid colours increase their chance to mate and this benefit outweighs the cost associated with predation risk (Promislow, Montgomerie & Martin, 1992). Similar 'colourful male' strategies have also been observed in some lizard species (Stuart-Fox *et al.*, 2003). Different strategies between sexes is not restricted to morphology, but also their ecology: habitat and resource partitioning have been observed in some birds (Lopez Ornat & Greenberg, 1990), and large mammals (Bleich, Bowyer & Wehausen, 1997; Weckerly, 1998). The concept of the reckless male and the rational female (Vesakoski, Merilaita & Jormalainen, 2008) may be explained by the high female parental investment and the costs associated, relative to that of the males (Emlen & Oring, 1977). Thus males may benefit from more risky behaviour and trade-off the costs of movement to search for mates to enhance their reproductive output (Trivers, 1972). Males of some species of snake exhibit mate-searching behaviour during the breeding season (Madsen & Shine, 1993; Madsen, 1984; Reinert & Zappalorti, 1988), which increases their risk of mortality (Aldridge & Brown, 1995). Mate searching is also present in some lizard species, where males have larger, overlapping home-ranges compared to females (Olsson, 1993). Male-biased dispersal may facilitate gene-flow between fragmented populations by moving further or crossing exposed habitats such as the transformed matrix.

Habitat destruction and fragmentation is a major concern for biodiversity conservation in South Africa (Raimondo & von Staden, 2009; Branch & Harrison, 2004). The Cape Floristic Region (CFR) of the Western Cape makes up one of 25 global biodiversity hotspots prioritised for conservation based on species endemism and the threat severity (Myers *et al.*, 2000). In the CFR, 69% of the fynbos biome remains and

only 10% is formally under conservation (Raimondo & von Staden, 2009). Most of the habitat transformation in the fynbos biome has occurred on the more fertile, and low-lying areas as a result of urban development or agriculture (Rebelo *et al.*, 2006). This threatens the conservation of the plant and animal species that occupy the lowlands of the fynbos biome. One such reptile, the Cape dwarf chameleon (*Bradypodion pumilum*), occurs within this region in the Western Cape (Tolley & Burger, 2007). This species is Red Listed as Vulnerable due to its small distribution, habitat loss, degradation and fragmentation of populations (Tolley, 2014). Although this species is known to exist in garden and vegetated suburban areas, these populations could be declining and studies are required to investigate their ability to persist (Tolley, 2014), especially with small, low income-housing and modern preference of paving. Around 1 300 km^2 (10%) of its distribution falls within protected areas (Tolley, 2014) and the remaining space has already, or is at imminent risk of being developed due to the rapidly increasing population of Cape Town and the growing demands for land (Rebelo *et al.*, 2011; Holmes *et al.*, 2012).

The Cape dwarf chameleon's vulnerability to habitat fragmentation can be assessed by its ability to disperse. Dispersal is determined by a combination of movement distances and the type of habitats utilised. They "cruise" slowly through bushes while searching for food during the day (Butler, 2005). However, chameleons need to avoid predators: most commonly birds (such as shrikes and starlings), snakes (nocturnal and diurnal) and domestic cats (Tolley & Burger, 2007). They use vegetation as cover and a number of strategies to remain undetected by predators (Measey, Raselimanana & Herrel, 2013), making it unlikely that chameleons will expose themselves to predators by dispersing across open ground. Indeed, no Cape dwarf chameleons were observed while crossing open ground by Katz (2012) or during this study. It has been suggested that they perch higher while asleep at night than when active during the day so that predators cannot reach them or at least alert them from vibration caused by climbing predators (Measey, Raselimanana & Herrel, 2013). Conversely, during the day birds are their predominant predators and chameleons could perch lower in denser vegetation to reduce aerial detection. Thus predation is expected to restrict habitat use to vegetation with adequate cover, and different predators active at day and night could further constrain dispersal through vegetation of suitable height.

For a species to persist within its environment, individuals not only need to survive, but must also reproduce. Mate searching could be another factor that influences the distance moved by chameleons. Males of the Mediterranean Chameleon (*Chamaeleo chamaeleon*) were observed following or 'mate-guarding' females from other males (Cuadrado, 2006), suggesting that males are competing for females. Thus males of this species could be moving further than females in search of mates, but this has not been confirmed for *B. pumilum*. The Cape dwarf chameleon mates and reproduces aseasonally (Tolley et al. 2014), and males have been suggested to be more active (Butler, 2005) and may move further than females (Tolley *et al.*, 2010), which suggests a male-biased mate searching strategy. Mate searching has the potential to increase dispersal ability of the Cape dwarf chameleon as males could move further and risk predation by moving though more exposed vegetation in the search for mates.

Research on the fine-scaled genetic patterns, behaviour and ecology is lacking for the Cape dwarf chameleon (Hopkins & Tolley, 2011), making it difficult to assess the effects of habitat fragmentation on this species. However, more recent studies are addressing this lack of information and have targeted the chameleon population from Noordhoek wetlands in the Western Cape. In these wetlands, Katz, Tolley & Altwegg (2013) found that high reproductive capacity of this species allows the population recovery from high mortality and results in large population fluctuations, allowing them to persist in disturbance-prone habitats. Another study of the same population revealed rapid shifts in allele frequencies over a few years, suggesting considerable movement of chameleons between the study site and the rest of the wetlands (Katz, Tolley & Bishop, 2013). Although there is evidence of some dispersal and gene-flow at the Noordhoek Wetlands, it is still unknown how far these chameleons move and which habitat or vegetation characteristics encourage this movement.

In this study the habitat utilisation and movement of the Cape dwarf chameleon is investigated. It is hypothesised that males of this species utilise a larger MCP area and move greater distances than females, because of their need to locate potential mates. In addition, habitat use, such as perch size, height and cover, was compared between males and females to investigate resource or niche partitioning relating to mate searching or perhaps predator avoidance. Furthermore, the difference in habitat use between day and night was investigated to determine if it is in agreement with a predator avoidance strategy. Chameleons should perch in denser vegetation during the day than at night to avoid aerial predators and perch higher at night than during the day, in order to avoid terrestrial predators such as snakes. These hypotheses were tested by radio-tracking adult chameleons in the Noordhoek Wetlands, and thus assess the vulnerability of the Cape dwarf chameleon to habitat fragmentation.

MATERIALS AND METHODS

Study area

The study was conducted within the Noordhoek Wetland (34°06'43"S, 18°22'44"W, <10 m a.s.l.), situated on the Cape Peninsula, Western Cape, South Africa (Figure 1). The study site was on the eastern corner of the wetland which is surrounded by sports fields and grazing fields, roads and suburbia to the north, east and south. The study site has transformed from an open, sandy area in 1988 to being covered in vegetation (Figure 2). The wetland spans from Klein Slangkop to Chapman's Peak over an area of roughly 340 ha (Anon, n.d.). The vegetation within the study site consisted of mainly thatching restio (*Elegia tectorum*), but with sedges (*Cyperaceae*) and common reeds (*Phragmites australis*) abundant in the waterlogged depressions. Other species distributed amongst the restios included Tabakbos (*Senecio halimifolius*), yellow Everlasting (*Athanasia dentata*), Bakbos (*Nidorella ivifolia*) and Vaaltee (*Plecostachys serpyllifolia*). The slightly elevated, dry sandy patches had Blomboss (*Metalasia muricata*) with other vegetation that provided little cover, such as smaller restios and bushes. Invasive alien plants are present, such as the *Acacia saligna*, but these are sparse. The substrate was of loose white sand which was only exposed on the raised patches and footpaths. Pedestrians, dogs and horse-riders frequently bisect the wetland along the footpaths. The study area is flooded during winter after heavy rainfall and water flows from a drainage pipe in the west of the site. This area has been the study site for previous *Bradypodion pumilum* studies, see Katz, Tolley & Bishop (2013), Katz, Tolley & Altwegg (2013) and Tolley et al. (2010) for further details on the site.

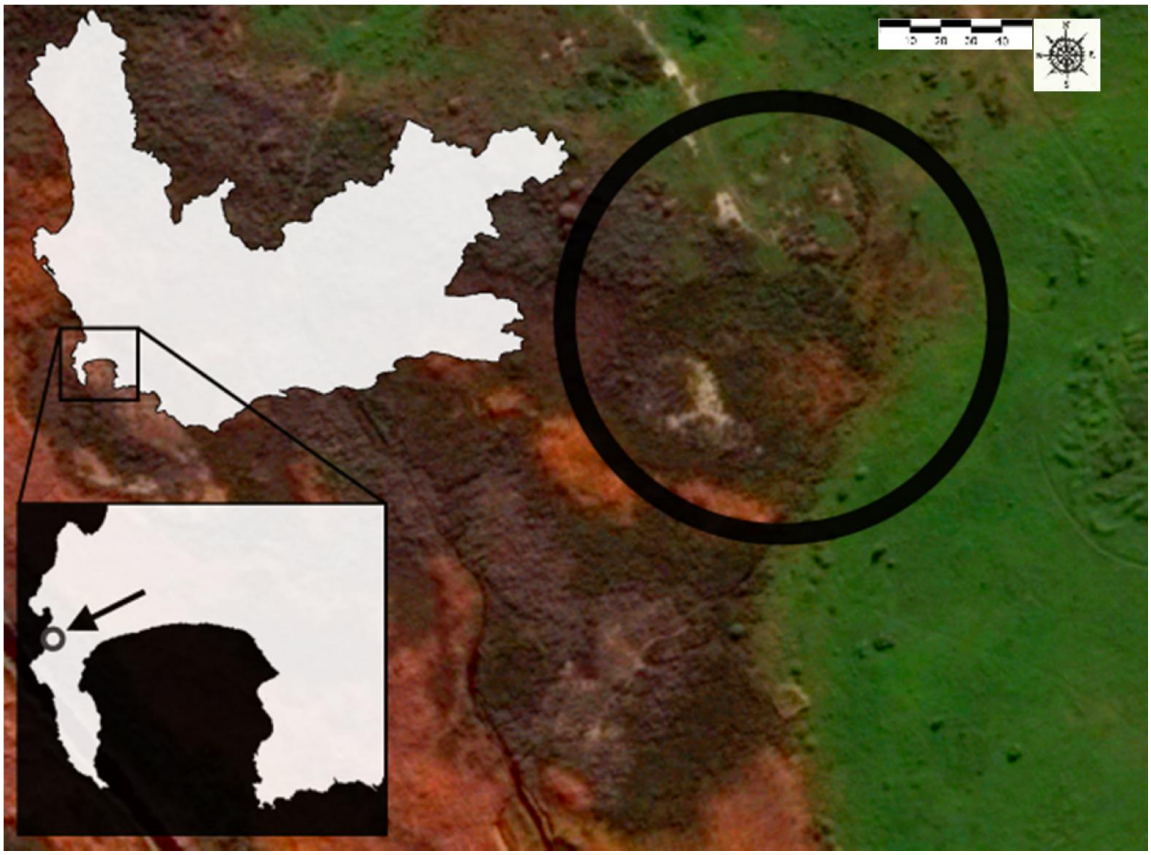

Figure 1. The location of the Noordhoek Wetlands in the Western Cape (grey circle), and a Google Earth image showing the position of the study site (black circle).

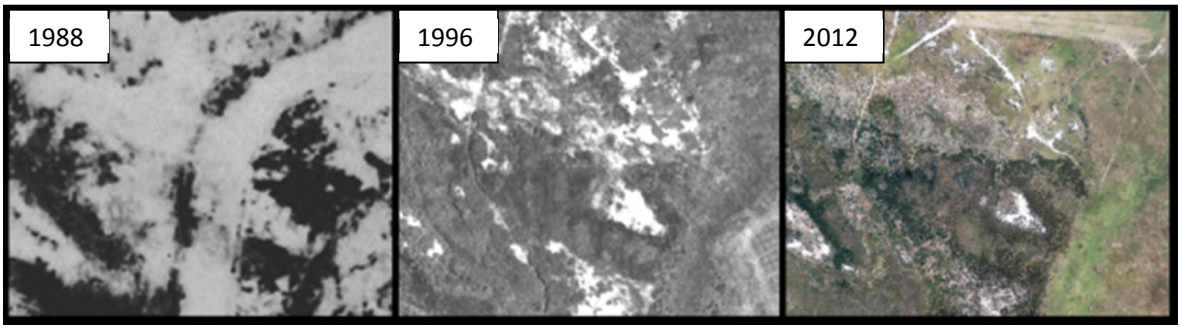

Figure 2. City of Cape Town aerial imagery showing vegetation change over time at the study site in Noordhoek Wetlands, Western Cape.

Radio-tracking

Cape dwarf chameleons (*Bradypodion pumilum*) were radio-tracked during autumn in March 2010 and April 2014. Data collection in 2010 was carried out by Eric Katz for his MSc (Katz, 2012). During both sampling periods chameleons were collected from Noordhoek Wetlands at night. In April 2014, torches were used to locate and select eight healthy adult chameleons, of equal sex ratio, six for radio-tracking and two for backup. Chameleons were placed inside a marked cloth bag for transport. Chameleons were processed on the same night of capture in a controlled environment. Each individual was weighed, measured, photographed and marked using a felt-tipped pen. The radio-transmitters were then activated and attached using Histoacryl® tissue adhesive (Aesculap®). The six transmitters used in 2010, Holohil Systems Ltd. model BD-2 (0.65g), were attached to the mid-dorsal ridge with a custom made saddle (Cuadrado *et al.*, 2001). In 2014 the six transmitters, Holohil Systems Ltd. Model LB-2X (0.27g), were attached directly to the upper side of the chameleon, with the antenna pointing back and slightly upwards (Figure 3). One of the 2014 transmitters malfunctioned, thus only five chameleons could be radio-tracked. Chameleons were placed within Exo Terra® Quick-Release Full Screen Terrarium with vegetation and observed for signs of attachment failure or excessive stress.

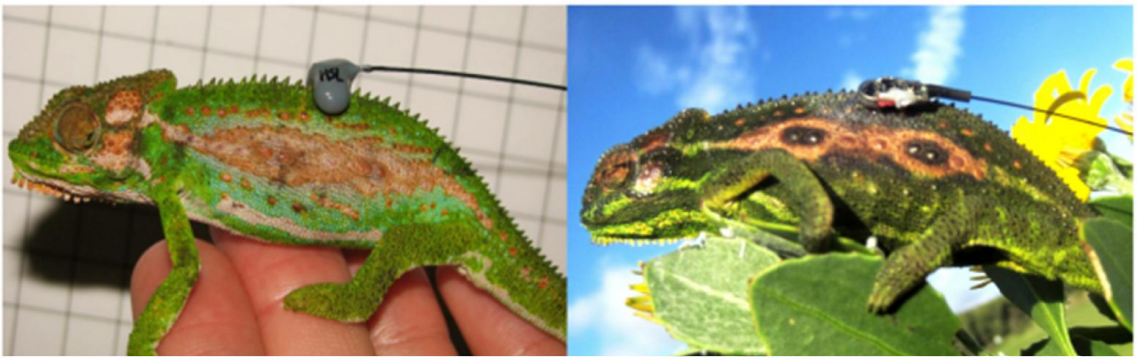
Figure 3. The radio-transmitters and their placement on Cape dwarf chameleons captured at the Noordhoek wetland, South Africa, in 2010 (left) and 2014 (right). Photos Krystal Tolley.

The chameleons were kept overnight and through the next day for further observation. The cages were kept in the shade throughout the day and were regularly sprayed with water and monitored. All chameleons were release at their original location of capture, prior to dusk. Radio-tracking beginning the following day,

chameleons were located using a radio receiver: model TRX-1000WR (Wildlife Materials Inc.), antenna and headphones. Each transmitter was set to a unique frequency within the range of 150.0-150.1 Hertz. The chameleons were honed in by crude methods of triangulation, moving perpendicular to the signal or rotating the antenna until the intensity of the transmission increased and a direction acquired. Radio-tracking began the day after release and continued for 10 days. Radio-tracking began every morning at 7:30 and ended around 16:30 from the 20th - 29th April in 2014, with tracking details in 2010 described by Katz (2012). In 2014, on average chameleons were tracked hourly. The perch height, diameter, vegetation cover and GPS position were recorded for each observation. At the end of the study the chameleons were recaptured, weighed and their transmitters removed.

Every hourly recapture for all radio-tracked chameleons included a measurement of the chameleon perch height, measured using a metre stick and estimated to the nearest 10cm. Additionally, the perch plant species was recorded and the stem diameter of the plant held by the chameleon was measured using digital callipers and the total diameter was measured if the chameleon was clasping multiple stems. The closest and most accessible stem held by any of the chameleon's feet was measured. Finally, the vegetation cover directly surrounding the chameleon was recorded by photographing a coloured 15x15cm plastic square placed 10-15cm behind the chameleon and at arm's length from the digital camera (Figure 4). The vegetation cover was then estimated using the image editing program Paint.NET by removing the visible yellow background from the vegetation and calculating the area covered.

Figure 4. The method used to measure vegetation cover. A picture is taken of the yellow square (left) and this is converted into a dichromatic image and the cover is calculated (right).

Nocturnal habitat use

Night-time chameleon surveys, collected by Tolley, Raw and Katz from 2008 to 2010 in the Noordhoek wetlands, were used to compare night vegetative use of chameleons to daytime radio-tracking. During night surveys the chameleon sex, perch diameter and perch height were documented following capture using torches to locate chameleons. In addition to 2008-2010, night surveys were conducted at the study site on the 2nd and 5th May 2014, a week after the radio-transmitter removal. Unlike the previous night surveys, chameleons were located by an intensive top-down torch search of vegetation to reduce bias from sampling the most visible chameleons. Perch height and vegetation cover were recorded for the total of ten chameleons located over these two nights. Rain-free nights were selected for these two night surveys to minimise effects of weather differences between the radio-tracking and night searching data.

Vegetation survey

After completing the radio-tracking, vegetation transects were conducted at the study site. Straight lines were sampled through areas used by the radio-tracked chameleon. At every two metre interval the closest vegetation was selected at 0.7 m above the ground and at 0.4 m where vegetation was shorter than 0.7 m. The diameters for the first 12 stems, on average, were measured at each interval and each plant species was documented. The stem diameters were averaged and proportion of plant species calculated per interval for all transects to eliminate bias arising from oversampling a particular transect interval. The radio-tracked chameleon perch diameters were compared to those recorded in the vegetation survey was compared using a non-parametric Wilcoxon test. Furthermore, the plant species selected by the radio-tracked chameleons were compared with those documented in the vegetation transect.

Area of utilisation calculation

Areas of utilisation were constructed from the 2010 and 2014 radio-tracked chameleons using the minimum convex polygon (MCP) method (Eddy, 1977). The areas of utilisation for each chameleon were cumulatively calculated for number of days followed. The first day of radio-tracking included five GPS positions per chameleon to obtain an initial MCP. The following days used the first (morning), middle (midday) and last (late afternoon) GPS positions to calculate the MCPs for each chameleon. The analysis was limited to three positions a day in order to standardise the datasets as the 2010 dataset only recorded three to five observations per day. The data were analysed using the program R (R Core Team 2013).The GPS coordinates were converted in spatial points using the R package ‘sp’ (Pebesma & Bivand, 2005). These were then transformed to Universal Transverse Mercator coordinates (UTM) by the R package ‘rgdal’ (Bivand, Keitt & Rowlingson, 2013). The MCPs were then calculated using the UTM coordinates for all chameleons over each cumulative day followed, using the R package ‘adehabitatHR’ (Calenge, 2006).

Daily displacement calculation

The net movement for each radio-tracked chameleon was calculated from the first and last recapture of every day. The analysis was limited to displacement rather than total movement due to few GPS positions recorded per chameleon per day in 2010. The GPS coordinates were converted into UTM coordinates using the process outlined in the previous paragraph and the daily displacement was calculated by subtracting the UTM coordinates. The time between the first and last recapture varied for different observations, but was included in the data analysis.

Data Modelling

Linear mixed effects models in the program R (R Core Team 2013) with the package 'lme4' (Maechler, Bolker & S, 2014) were used to determine the effect of relevant factors on the measurement of interest. To account for the repeated observations of radio-tracked chameleons, a random effect for the chameleon identity was included. For the area of utilisation model, the slope of area over time per chameleon was allowed to vary independently. The effect of chameleon sex on the dependent variables of area of utilisation, daily displacement, perch diameter, perch height and vegetation cover was modelled. In additionally, the effect of time of day and day versus night on chameleon perch diameter, perch height and vegetation cover were modelled, by combining the 2008-2010 and 2011 night surveys with the data from radio-tracking. A factor was included in preliminary modelling to ensure the 2014 and 2008-2010 night survey data were congruent. The perch height, diameter and vegetation cover for radio-tracked chameleons were separated into the time categories of morning (7:00-9:00), midday (9:00-13:00) and afternoon (13:00-16:00). Other explanatory variables were included in model selection, if relevant, such as chameleon snout-vent length, year of data collection or time of day. Maximum likelihood (ML) was used to fit the models and Akaike's Information Criterion (AIC) to select the most informative models. The residual variance of the selected model was checked and the dependent variable was log-transformed if necessary.

RESULTS

Area of utilisation

The movements and distribution of the six chameleons radio-tracked in 2010 and the five in 2014 were mostly confined to denser vegetation of the low-lying areas of the study site in Noordhoek wetlands (Figure 5). Two well supported mixed effect models for chameleon minimum convex polygon (MCP) area of utilisation were identified (A6 & A13; Table 1).The area of utilisation increased almost linearly over the duration tracked in both models, despite highly variable increase between individuals (Figure 6). Area of utilisation also scaled positively with chameleon snout-vent length in one model, but this was not statistically supported (Figure 7). Neither chameleon sex nor year of data collection had a detectable effect on the area of utilisation. The predicted area of utilisation for a chameleon of 70.81 mm (snout-vent length) over a 10 day period chameleon was 51.24 m^2 (±15.48 m^2 -excluding uncertainty from random slope).

Daily displacement

The predicted chameleon daily displacement for the 2010 and 2014 radio-tracked chameleons was 10.94 m (±2.28 m). The null model (B16) was clearly the best fit, with no explanatory parameters (Table 2). The daily displacement was log-transformed for the models due to the residual variation. Thus chameleon sex, chameleon snout-vent length, year of data collection and time between displacement observations had no detectable effect on daily displacement.

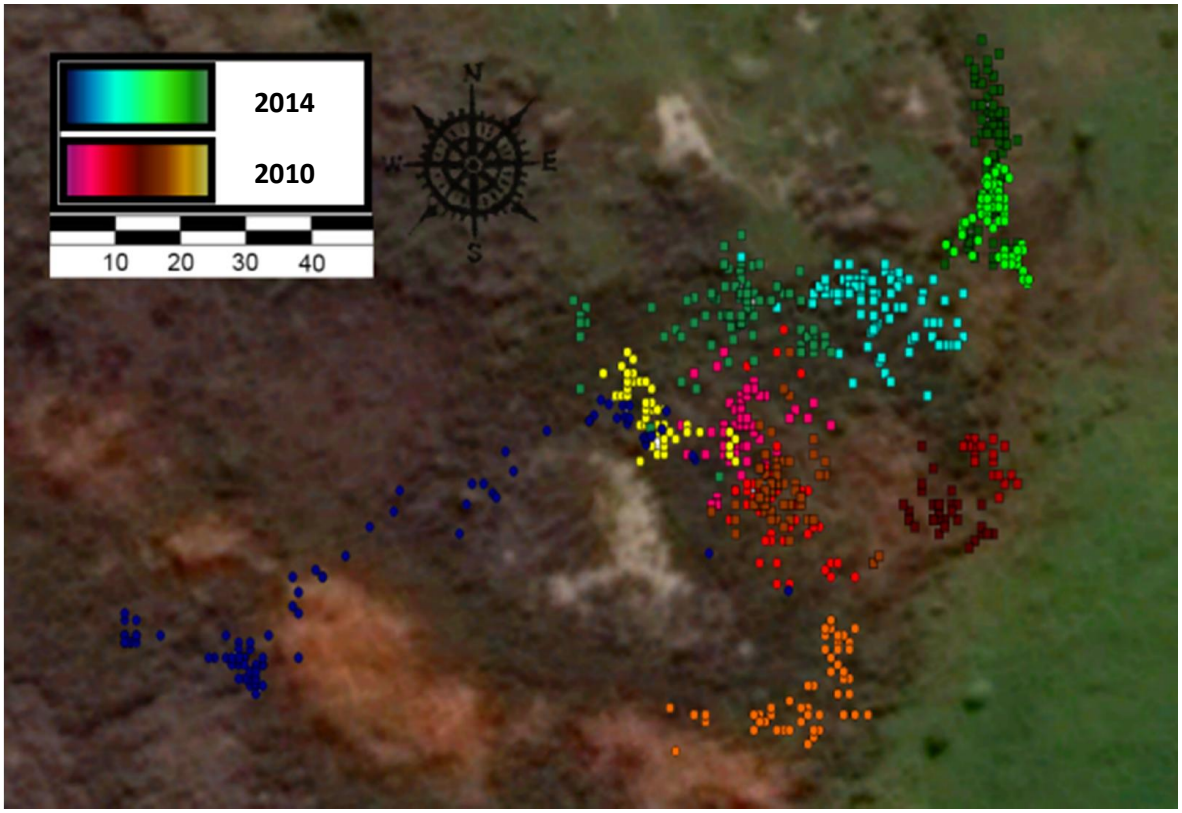

Figure 5. The spatial positions of radio-tracked chameleons during 2010 (brown-orange) and 2014 (blue-yellow) within the Noordhoek wetlands. Males are shown as squares and females as circles.

Perch diameter

Two models were well supported for the daytime perch diameter and both included chameleon snout-vent length, while one included chameleon sex (C2 & C5; Table 3). Thus the chameleon perch diameter increased with chameleon snout-vent length and males used thicker stems than females during the day, although the latter was not statistically supported (Figure 8). The other explanatory variable: time of day, had no detectable effect on perch diameter.

The model selection of perch diameter for chameleons at both day and night supported no explanatory variables (D6; Table 4). Thus chameleon sex, time of day or day versus night had no detectable effect on perch thickness when both daytime and night-time perch diameters were considered. Note that chameleon snout-vent length data was not collected in the 2008-2010 night surveys and thus was excluded as an explanatory variable from this model selection.

Perch height

Model selection for daytime perch height from the 2014 radio-tracked chameleons supported two models, both included sex and one additionally included time (E1 & E2; Table 5). Thus perch height decreased with vegetation cover. Male chameleons perch higher in the vegetation than females and this varied at a non-significant level for the time of day (Figure 9). The model selection for daytime and night-time perch height also supported two models, both included day versus night and one included sex (F1 & F2;

Table **6**). Thus at night, males and females displayed little difference in perch height, but chameleons generally perched higher at night than during the day (Figure 10).

Perch vegetation cover

The model selection for chameleon perch vegetation cover during the day was weakly supported by all models (Table 7). Female chameleons perched in thicker vegetation cover than males, although this was not statistically supported, and variation between morning, midday and evening were negligible (Figure 11). The model selection for perch cover including both day and night supported two models, both included day versus night and one included sex (H1 & H2; Table 8). Chameleons perched in denser vegetation cover during the day than at night and females perched in denser vegetation than males, although not statistically supported (Figure 12).

Perch selection

The radio-tracked chameleons of 2014 perched on significantly thicker plant stems than what was available at random as indicated by the vegetation transects ($W=0.67$, $p<0.0001$; Figure 13). The high frequency of thatching restio (*Elegia tectorum*) being used as perches by radio-tracked chameleons in 2014 can be explained by their dominance within the vegetation transects and none of the plant species recorded during the random transect were completely avoided (Figure 14). One radio-tracked chameleon spent a couple days

in low vegetation characterised by sparse sedges, *Cynodon* grass, *Nidorella ivifolia* and *Orphium frutescens*, but eventually returned the taller and denser restios.

Table 1. Summary of model selection for Cape dwarf chameleon (*Bradypodion pumilum*) area of utilisation over consecutive days at the Noordhoek Wetlands, South Africa. Including Akaike's Information Criterion (AIC), number of parameters (K), maximum log-likelihood and best model(s) in bold. Model parameters and symbols: L (chameleon snout-vent length), T (duration tracked), S (sex) and Y (year of data collection: 2010 vs 2014). The random effects included the chameleon identity and gradient of the area of utilisation over duration tracked.

Model number	Model parameters	AIC	ΔAIC	AIC weight	K	Maximum log likelihood
A1	L+T+S+Y	932	3.28	0.05	9	-457.16
A2	L+T+S	931	2.00	0.09	8	-457.52
A3	L+T+Y	930	1.45	0.12	8	-457.24
A4	L+S+Y	939	9.95	0.00	8	-461.49
A5	T+S+Y	932	3.46	0.04	8	-458.24
A6	**L+T**	**929**	**0.00**	**0.24**	**7**	**-457.52**
A7	L+S	937	8.25	0.00	7	-461.64
A8	L+Y	937	7.97	0.00	7	-461.50
A9	T+S	931	1.75	0.10	7	-458.39
A10	T+Y	931	1.81	0.10	7	-458.42
A11	S+Y	938	9.31	0.00	7	-462.17
A12	L	935	6.26	0.01	6	-461.65
A13	**T**	**929**	**0.18**	**0.22**	**6**	**-458.60**
A14	S	937	7.73	0.01	6	-462.38
A15	Y	937	7.80	0.00	6	-462.42
A16	null	935	6.30	0.01	5	-462.67

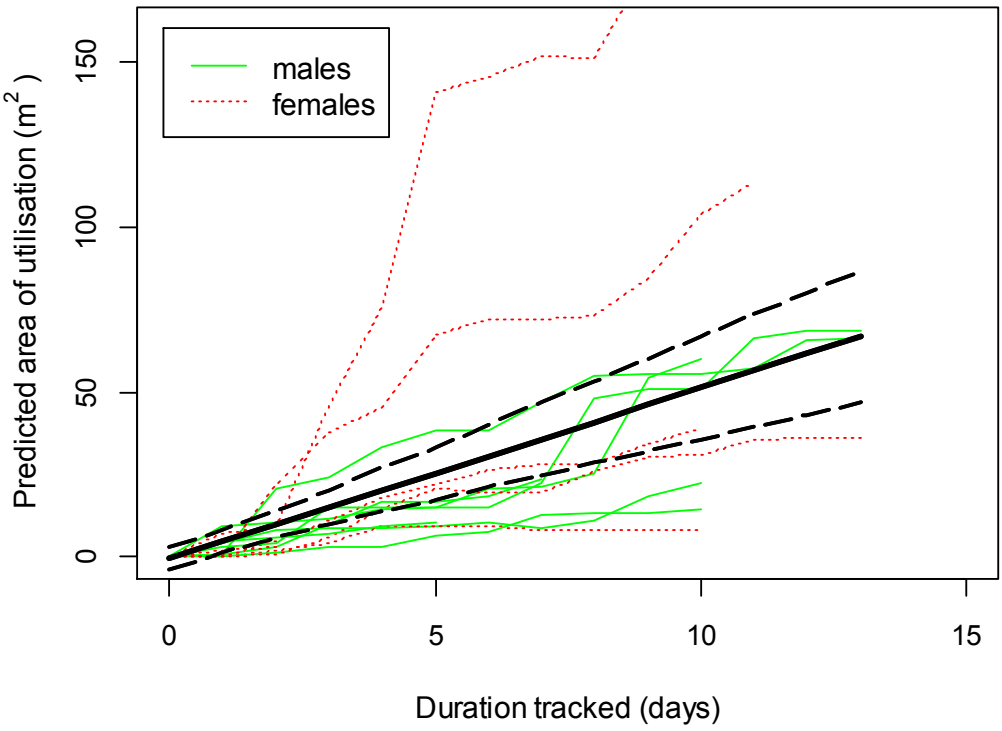

Figure 6. The Cape dwarf chameleon predicted area of utilisation over duration followed for the mean chameleon snout-vent length (63 mm), including 95% confidence intervals (dashed lines). Modelled using 2010 and 2014 radio-tracking data and predicted by model A6 in One **radio-tracked chameleon spent a couple days in low vegetation characterised by sparse sedges, *Cynodon* grass, *Nidorella ivifolia* and *Orphium frutescens*, but eventually returned the taller and denser restios.**

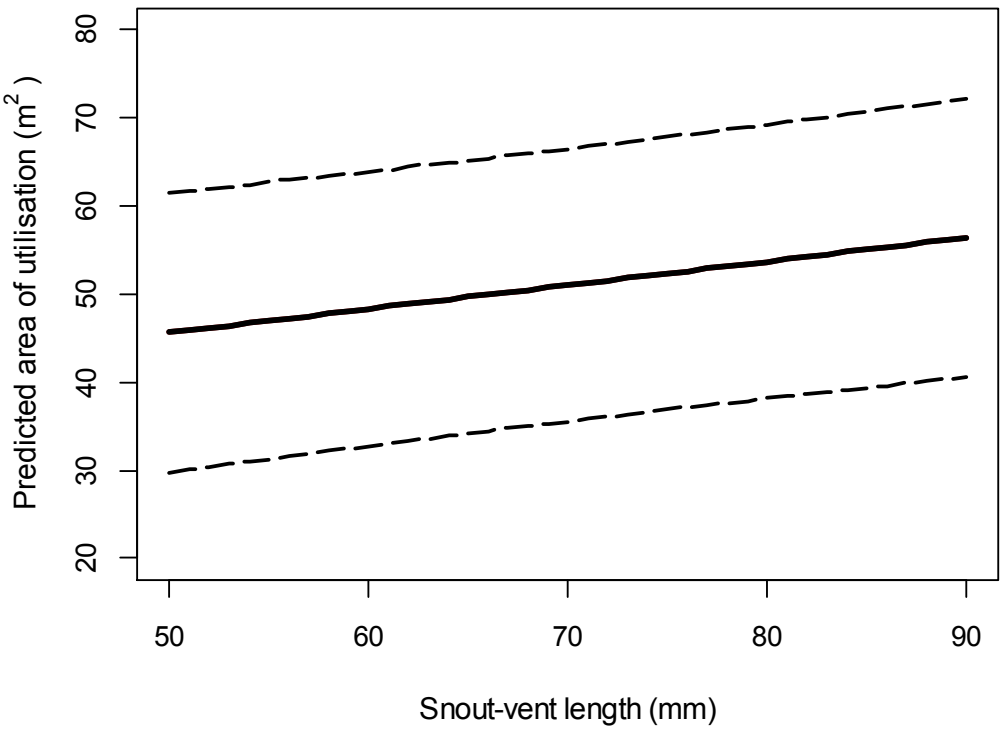

Figure 7. The Cape dwarf chameleon predicted area of utilisation over chameleon snout-vent length after 10 days of radio-tracking, including 95% confidence intervals (dashed lines). Modelled with the 2010 and 2014 radio-tracking data and predicted by model A6 in One **radio-tracked chameleon spent a couple days in low vegetation characterised by sparse sedges, *Cynodon* grass, *Nidorella ivifolia* and *Orphium frutescens*, but eventually returned the taller and denser restios.**

Table 2. Summary of model selection for Cape dwarf chameleon (*Bradypodion pumilum*) log-transformed daily displacement at the Noordhoek Wetlands, South Africa. Including Akaike's Information Criterion (AIC), number of parameters (K), maximum log-likelihood and best model(s) in bold. Model parameters and symbols: L (chameleon snout-vent length), S (sex), Y (year of data collection; 2010 vs 2014) and T (time between displacement observations). The random effects included the chameleon identity.

Model number	Model parameters	AIC	ΔAIC	AIC weight	K	Maximum log likelihood
B1	L+S+Y+T	691	6.43	0.01	7	-338.29
B2	L+S+Y	689	4.74	0.02	6	-338.44
B3	L+S+T	689	5.27	0.02	6	-338.70
B4	L+Y+T	689	4.44	0.02	6	-338.29
B5	S+Y+T	689	4.79	0.02	6	-338.46
B6	L+S	688	3.73	0.03	5	-338.94
B7	L+Y	687	2.76	0.06	5	-338.45
B8	L+T	688	3.39	0.04	5	-338.77
B9	S+Y	687	3.02	0.05	5	-338.58
B10	S+T	687	3.28	0.04	5	-338.71
B11	Y+T	687	2.95	0.05	5	-338.55
B12	L	686	1.94	0.09	4	-339.04
B13	S	686	1.88	0.09	4	-339.01
B14	Y	685	1.20	0.12	4	-338.67
B15	T	686	1.39	0.11	4	-338.77
B16	**null**	**684**	**0.00**	**0.22**	**3**	**-339.07**

Table 3. Summary of model selection for Cape dwarf chameleon (*Bradypodion pumilum*) perch thickness during the day at the Noordhoek Wetlands, South Africa. Including Akaike's Information Criterion (AIC), number of parameters (K), maximum log-likelihood and best model(s) in bold. Model parameters and symbols: L (chameleon snout-vent length), S (sex) and T (time of day: 7:00-9:00, 9:00-15:00, 15:00-17:00). The random effects included the chameleon identity.

Model number	Model parameters	AIC	ΔAIC	AIC weight	K	Maximum log likelihood
C1	L+S+T	1606	3.55	0.08	7	-795.76
C2	**L+S**	**1602**	**0.00**	**0.48**	**5**	**-795.98**
C3	L+T	1606	4.05	0.06	6	-797.01
C4	S+T	1616	13.54	0.00	6	-801.75
C5	**L**	**1603**	**0.54**	**0.37**	**4**	**-797.25**
C6	S	1612	10.07	0.00	4	-802.02
C7	T	1614	11.57	0.00	5	-801.77
C8	null	1610	8.09	0.01	3	-802.03

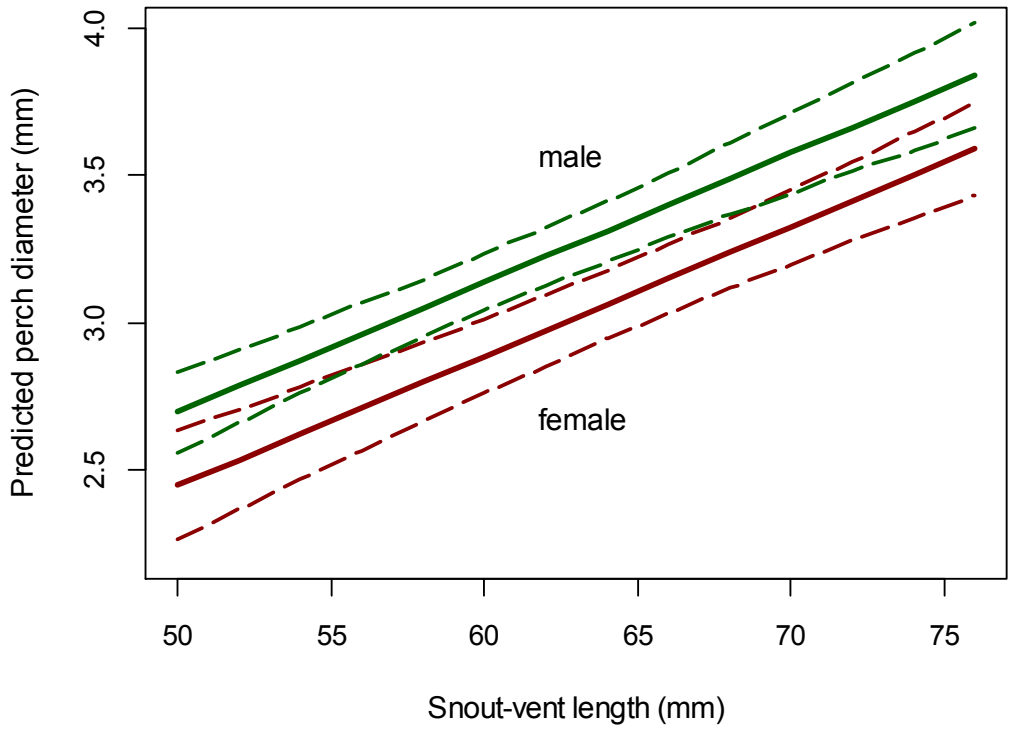

Figure 8. Predicted chameleon perch diameter over snout-vent length for both sexes of the Cape dwarf chameleon, including 95% confidence intervals (dashed lines). Modelled using the 2014 radio-tracked chameleon data and predicted with model C2 in Table 3.

Table 4. Summary of model selection for Cape dwarf chameleon (*Bradypodion pumilum*) perch thickness between day and night at the Noordhoek Wetlands, South Africa. Including Akaike's Information Criterion (AIC), number of parameters (K), maximum log-likelihood and best model(s) in bold. Model parameters and symbols: S (sex) and T (time of day: 7:00-9:00, 9:00-15:00, 15:00-17:00, 21:00-24:00) or D/N (day versus night). Chameleon snout-vent length was excluded as an explanatory variable as it was absent from the 2008-2010 night surveys. The random effects included the chameleon identity.

Model number	Model parameters	AIC	ΔAIC	AIC weight	K	Maximum log likelihood
D1	S+T	3716	6.93	0.02	7	-1851.13
D2	T	3714	4.95	0.04	6	-1851.14
D3	S	3711	1.99	0.19	4	-1851.66
D4	S+D/N	3713	3.95	0.07	5	-1851.64
D5	D/N	3711	1.96	0.19	4	-1851.64
D6	**null**	**3709**	**0.00**	**0.50**	**3**	**-1851.66**

Table 5. Summary of model selection for Cape dwarf chameleon (*Bradypodion pumilum*) perch height during the day at the Noordhoek Wetlands, South Africa. Including Akaike's Information Criterion (AIC), number of parameters (K), maximum log-likelihood and best model(s) in bold. Model parameters and symbols: S (sex) and T (time of day: 7:00-9:00, 9:00-15:00, 15:00-17:00). The random effects included the chameleon identity.

Model number	Model parameters	AIC	ΔAIC	AIC weight	K	Maximum log likelihood
E1	**S+T**	**3875**	**0.36**	**0.29**	**6**	**-1931.58**
E2	**S**	**3875**	**0.00**	**0.35**	**4**	**-1933.40**
E3	T	3886	11.04	0.00	5	-1937.92
E4	null	3886	10.78	0.00	3	-1939.79

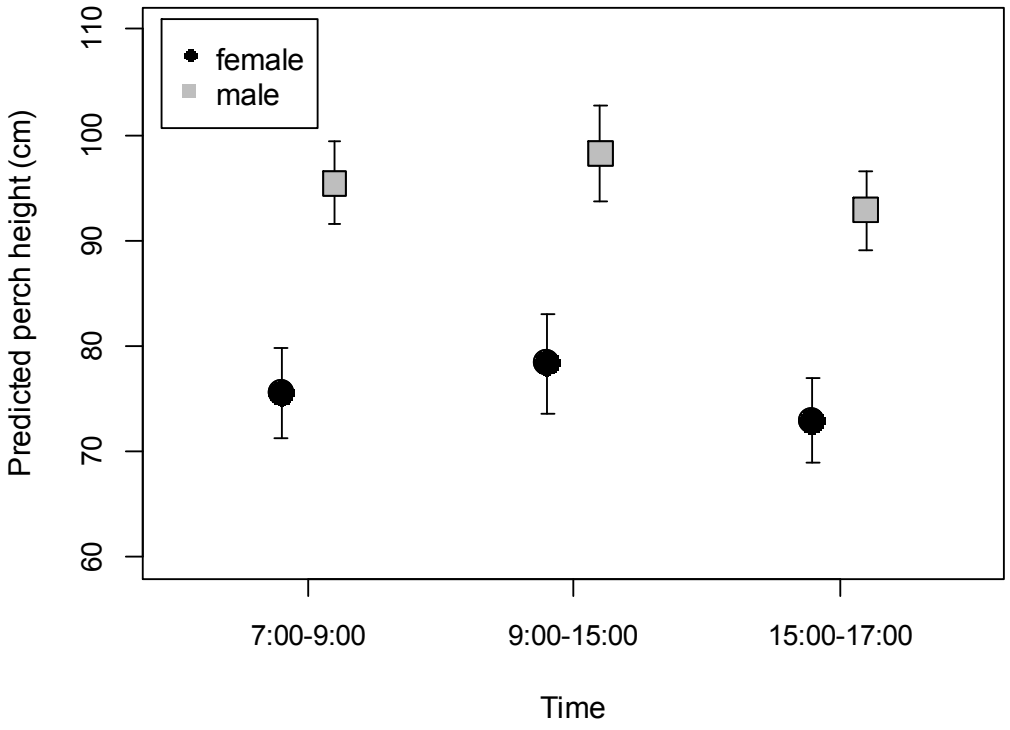

Figure 9. The predicted chameleon perch height above ground during the morning, midday and afternoon for both sexes of the Cape dwarf chameleon, including 95% confidence intervals. Modelled with the 2014 radio-tracking data and predicted by model E1 in Table 5.

Table 6. Summary of model selection for Cape dwarf chameleon (Bradypodion pumilum) perch height between day and night at the Noordhoek Wetlands, South Africa. Including Akaike's Information Criterion (AIC), number of parameters (K), maximum log-likelihood and best model(s) in bold. Model parameters and symbols: S (sex) and D/N (time: day, night). The random effects included the chameleon identity.

Model number	Model parameters	AIC	ΔAIC	AIC weight	K	Maximum log likelihood
F1	**S+D/N**	**7928**	**1.12**	**0.30**	**5**	**-3958.97**
F2	**D/N**	**7927**	**0.00**	**0.52**	**4**	**-3959.42**
F3	S	7932	5.53	0.03	4	-3962.18
F4	null	7931	4.47	0.06	3	-3962.65

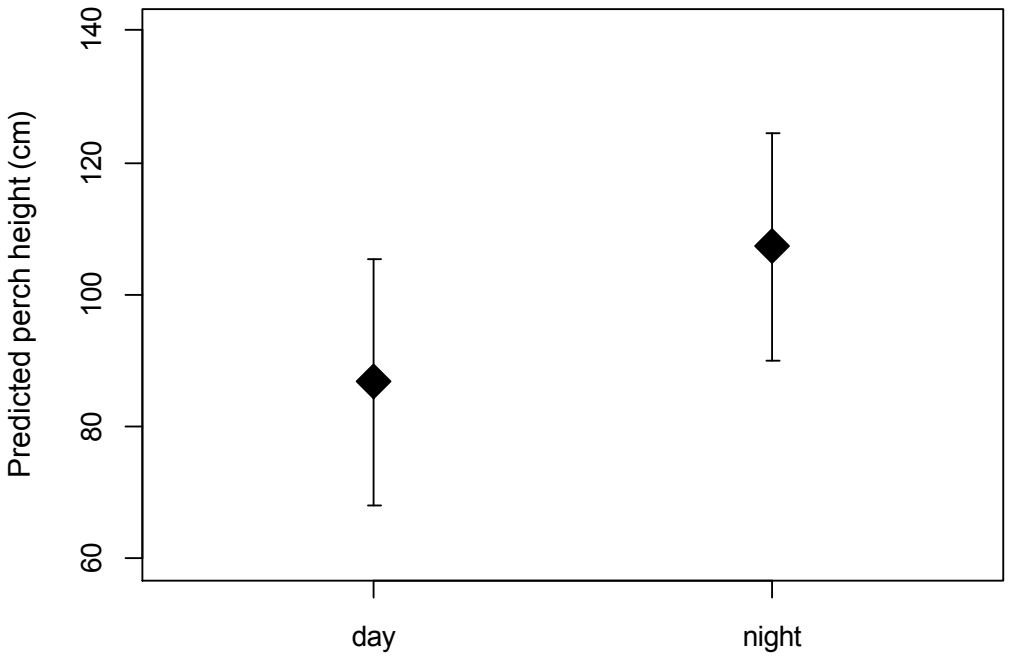

Figure **10**. The predicted Cape dwarf chameleon perch height above ground for day and night, including 95% confidence intervals. Modelled with 2014 radio-tracking and 2008-2011 night survey data and predicted by model F2 in

Table 7. Summary of model selection for Cape dwarf chameleon (*Bradypodion pumilum*) perch vegetation cover during the day at the Noordhoek Wetlands, South Africa. Including Akaike's Information Criterion (AIC), number of parameters (K), maximum log-likelihood and best model(s) in bold. Model parameters and symbols: S (sex), and T (time of day: 7:00-9:00, 9:00-15:00, 15:00-17:00). The random effects included the chameleon identity.

Model number	Model parameters	AIC	ΔAIC	AIC weight	K	Maximum log likelihood
G1	S+T	-274	0.45	0.13	6	142.91
G2	T	-274	0.00	0.17	5	142.14
G3	S	-274	0.46	0.13	4	140.91
G4	null	-274	0.02	0.17	3	140.13

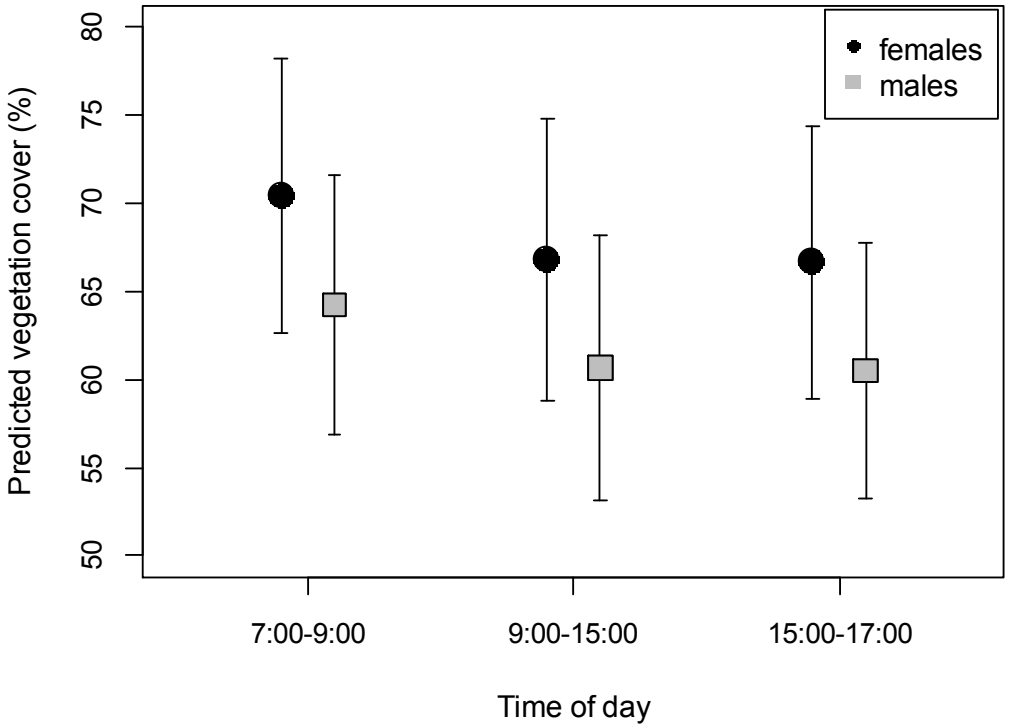

Figure 11. The predicted perch vegetation cover during the morning, midday and afternoon for both sexes of the Cape dwarf chameleon, including 95% confidence intervals. Modelled using 2014 radio-tracking data and predicted by model G1 in Table 7.

Table 8. Summary of model selection for Cape dwarf chameleon (*Bradypodion pumilum*) perch vegetation cover between day and night at the Noordhoek Wetlands, South Africa. Including Akaike's Information Criterion (AIC), number of parameters (K), maximum log-likelihood and best model(s) in bold. Model parameters and symbols: S (sex), and D/N (day versus night). The random effects included the chameleon identity.

Model number	Model parameters	AIC	ΔAIC	AIC weight	K	Maximum log likelihood
H1	**S+D/N**	**-278**	**0.00**	**0.60**	**5**	**143.99**
H2	**D/N**	**-277**	**0.85**	**0.39**	**4**	**142.56**
H3	S	-265	13.39	0.00	4	136.30
H4	null	-267	11.46	0.00	3	136.26

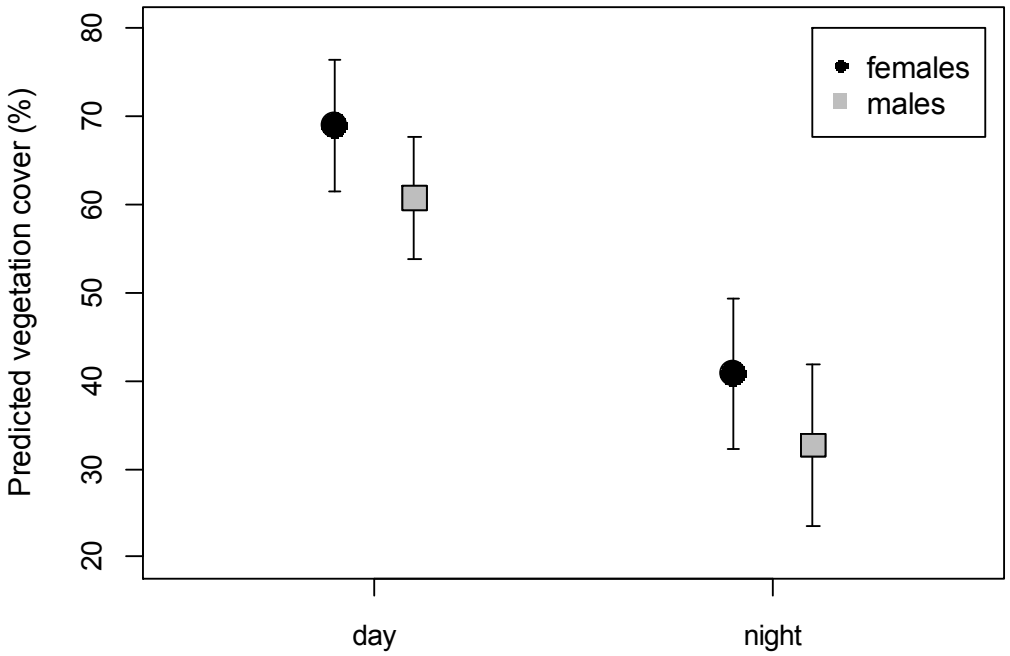

Figure 12. The predicted perch vegetation cover between day and night for both sexes of the Cape dwarf chameleon, including 95% confidence intervals. Modelled using 2014 radio-tracking data and 2014 night survey and predicted by model H1 in Table 8.

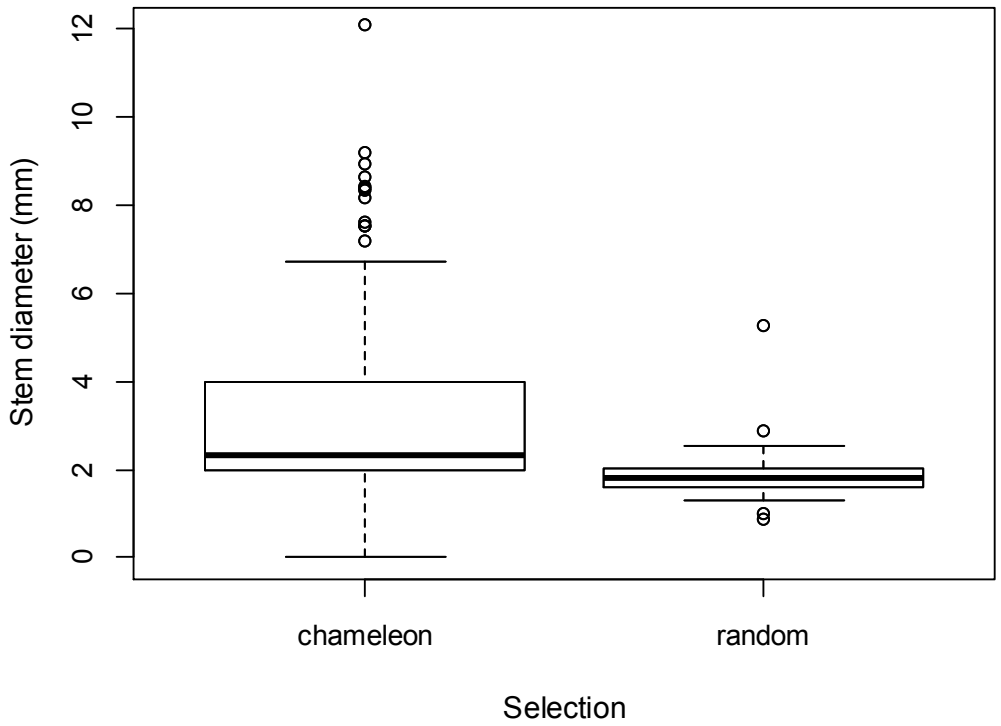

Figure 13. Box and whisker plots of the plant stem diameter for the 2014 radio-tracked chameleons (left) and the random vegetation transects (right).

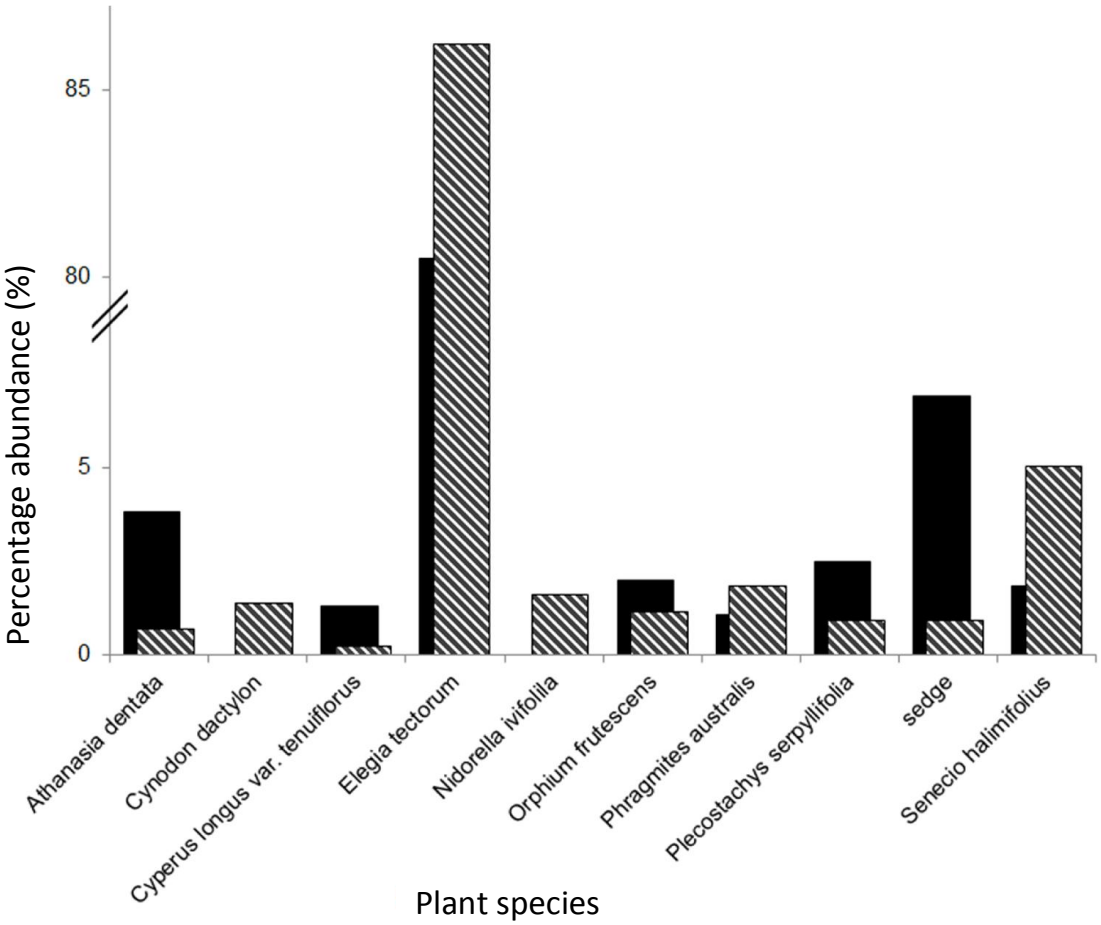

Figure 14. The percentage proportional abundance of the plant species recorded in the random vegetation transects (black) and those selected by the 2014 radio-tracked Cape dwarf chameleons (striped).

DISCUSSION

Key findings:

The radio-tracked Cape dwarf chameleons expanded their distribution across the wetlands at roughly constant rate over the study period. Some individuals moved within a particular direction, showing potential for substantial dispersal over longer periods. Chameleons avoided open areas with sparse, low-lying vegetation or bare sand; however, some must have occasionally crossed short distances over open ground between isolated bushes. Some males were observed following, mating or mate guarding female chameleons. However, males and females occupied similar sized areas and showed similar daily displacement. Males tended to perch higher than females during the day, which could benefit mate-guarding or mate-searching males. Chameleons perched higher and in lower vegetation cover at night than during the day. This could minimise risk of predation by birds in the day and snakes at night.

Chameleon movement

Remarkably, chameleons did not stay within the same area, but continued to expand their utilised areas at a relatively constant rate over the duration of the study. These areas of utilisation varied considerably among individuals over the ten day period, ranging from 10 to over 100 m^2. Although the Cape dwarf chameleon is aggressive towards conspecifics that get too close (Tolley & Burger, 2007), there was clearly movement within the areas used by conspecifics. The radio-tracked chameleons only represent a fraction of the population at the study site, implying that they frequently move through areas utilised by other chameleons. This is in conflict with territorial behaviour, as territorial animals defend a set area, which these chameleons clearly did not. The Mediterranean Chameleon has been described to sometimes have a 'mobile territory', where males defend the area surrounding a female from other males (Cuadrado, 2006). The Cape dwarf chameleon either has similar mobile territories or else lacks territories altogether.

The radio-tracked chameleons had a displacement of about 11 m during the day, which is low compared to some of the quick terrestrial lizards that can cover that distance in a fraction of the time (Avery, Bedford & Newcombe, 1982; Garland, 1999). However, although they are relatively slow, these chameleons are capable of covering large distances over time. During radio-tracking in 2010 and 2014, one individual on each occasion dispersed out of the core site and into the surrounding wetlands. Such occasional dispersal events combined with the lack of territorial boundaries supports the rapid shifts in allelic frequencies observed by Katz, Tolley & Bishop (2013), as chameleons would easily be capable of emigrating into the surrounding wetlands. This could also explain the apparent decreased survival of chameleons, from capture-mark-recapture by Tolley et al. (2010), on the edge of the study site in the Noordhoek wetlands. The mobility of this species over time could be a strategy that evolved in response to fire. The Cape dwarf chameleon appears to be absent in fire-prone areas, such as Silvermine, Cape Peninsula (Tolley, pers. comm.), but are often present in adjacent fire sheltered areas, such as forested ravines and strandveld, including gardens. Thus mobile individuals could benefit when they encounter a non-competitive environment created after

fire. They will not have to compete with adults for space or foraging and could return as large adults ready to mate. This could also facilitate repopulation of the chameleon populations in areas wiped out by an occasional large fire, when the vegetation has recovered.

Another interpretation of the observed movement patterns is that the duration of radio-tracking was not sufficient to show chameleons remaining within the same area. However, this explanation seems unsatisfactory, as the one radio-tracked chameleon moved rapidly and directly out of the study area, suggesting that it was dispersing, rather than slowly cruise foraging. The Cape dwarf chameleon shows a high potential for extensive migration between the study site and the remainder of the Noordhoek wetland.

Sex-biased dispersal

Male and female chameleons utilised similar areas over ten days of tracking and displaced similar distances during the day. This opposes the hypothesis that males move further distances than females to locate potential mates. This was previously supported in other studies either through greater activity or distance modelled using capture-mark-recapture (Butler, 2005; Tolley *et al.*, 2010), but Katz, Tolley & Altwegg (2013) found similar distances moved for both sexes when investigating a larger capture-mark-recapture dataset. These chameleons already cruise the vegetation while foraging for prey (Butler, 2005), and thus may not require mate-searching as they could encounter conspecifics on a regular basis. Alternatively, males could be searching for females, but the subsequent period of following and guarding could conceal the distance travelled by males during searching. Indeed, one of the radio-tracked males followed one of two females over the duration of the study. Regardless of whether males do search for females, our results show that males and females move similar distances.

In addition to mate following, one of the radio-tracked males encountered a male guarding a female, of which the male proceeded to attack the intruding male, eventually driving it off. This appears to be a behaviour described as mate guarding in the Mediterranean Chameleon, where males would follow and guard a female until mating occurred and then leave a couple of days later to search for others females (Cuadrado, 2006). The one radio-tracked Cape dwarf chameleon male followed a female chameleon for four days before mating, and then the following day the female moved away and the male found and began following a second female. However, another radio-tracked female was found mating with a random male that had not been previously observed; after mating the female moved rapidly out of the study site. Thus both females moved away from the male following mating. It is possible that they became gravid and were no longer interested in mating, which has been observed in the Mediterranean Chameleon where gravid females seem to aggressively deny males the opportunity to mate (Cuadrado, 1999). These post-mating movements could also have masked any differences in distance moved caused by mate-searching behaviour in males.

Sexual habitat preference

Male chameleons perched higher in the vegetation than females during the day. Perching higher during the day could be harmful by exposing chameleons to aerial predators such as birds or strong winds. However, perching higher could yield benefits to some chameleons by exposing them to more sunlight for thermoregulation or by having a better viewpoint. Chameleons need to thermoregulate like other lizards, but if perch height influences body-temperature then they should move lower down in the vegetation at midday when warm enough. Our results show no distinct height differences for morning, midday or afternoon chameleon perches, suggesting that this theory is unlikely, however, the temperatures were relatively mild in March-April. Male chameleons of one of the *Bradypodion melanocephalum-thamnobates* populations perched higher and in greater cover than the females (da Silva & Tolley, 2013). It is likely that these differences in perch height are relevant to a sexually related behaviour. Male chameleons that occupy superior viewpoints could locate potential mates more easily or oversee a nearby female for signs of sexual receptiveness and approaching rival males.

Females tended to perch in denser vegetation than males, but this was not statistically supported. This could be an effect of males perching higher as the vegetation gets less dense towards the top. There was similarly no detectable change for vegetation cover used by chameleons between morning, midday and afternoon. This suggests that either some constant factor is encouraging chameleons to remain in dense vegetation or that the vegetation cover is relatively homogeneous throughout the vegetation. This is contrary to the findings of da Silva & Tolley (2013), that found males perching in greater cover, however, they measured vertical cover using a spherical densiometer which explains the greater cover because males were perching higher in larger trees.

The chameleon perch diameter was thicker for males than females during the day, although this was not statistically supported. Thin perches are inadequate as they will not support the full weight of a chameleon and the grip strength is compromised for thick stems that chameleons struggle to enclose their hands around (Herrel *et al.*, 2011). However, chameleon size was taken into account and thus cannot explain differences between males and females. Male chameleons have relatively larger hands (Hopkins & Tolley, 2011) and a stronger grip than females (Herrel *et al.*, 2011), thus supporting the sexual difference. It has been suggested by Silva & Tolley (2013) that grip strength could be important in aggressive behaviour between conspecifics, which for males could determine whether they will mate with a female. It is also possible that male chameleons are clutching more restio stems in their hands because they tend to perch higher than females. Restios flex more easily the longer they area and thus could collapse to the ground if enough weight is applied. Additionally, perching higher could also increase exposure to stronger wind, requiring more support from either thicker or multiple stems.

Temporal habitat preference

Chameleon perch thickness was similar during the day and at night. This suggests that night-time perch diameters can be used as a substitute in studies for day time perch diameters. They also perched higher at night than during the day, which suggests that habitat utilisation is influenced by the risk of predation. By perching higher at night while sleeping, chameleons could be unreachable by snakes (Measey, Raselimanana & Herrel, 2013) and could have more time to become alerted to a climbing predator. It is unlikely that chameleons would climb higher at night when they are active during the day at lower levels, if no benefit existed. Furthermore, perching higher at night could expose chameleons to stronger winds and greater swaying of restio stems, increasing the risk of becoming dislodged. Thus it appears that chameleons are altering their use of vegetation to compensate for their vulnerability to terrestrial predators during their sleep. However, the 2008-2010 night surveys could have introduced searching bias, resulting in the higher, more exposed chameleons being sampled.

The vegetation cover of chameleon perches was higher during the day than at night surveys. This could be an effect of perching higher at the tops of vegetation at night and perching lower, in dense vegetation during the day. Chameleons perching at such exposed positions during the day could be quickly seen and eaten by birds, of which there is no equivalent predator at night. Eagle owls are unlikely to prey on chameleons at night, as these owls perch on the lookout for signs of movement (Roberts *et al.*, 2005) while chameleons are already asleep. Thus chameleons could be perching lower during the day to reduce exposure to birds. However, without experimentation it is difficult to distinguish between the benefits of predator avoidance and foraging efficiency, as chameleons are active during the day. Furthermore, vegetation cover was only introduced into the sampling method by 2014 and thus requires a larger sample size for night perches to confirm the observed trends.

Preferred vegetation

Chameleons perched on thicker branches than the stems sampled in the vegetation transects. This difference is most certainly due to the chameleon tendency to grasp multiple branches, especially of restios, at once. Restios have particularly numerous thin, long stems that are densely packed and each stem can easily collapse under a small weight. Thus it is likely that adult chameleons grab multiple stems for greater support and possibly to reduce swaying in the wind. Chameleons were found most often on the thatching restio (*Elegia tectorum*), which was also the most abundant plant species in the area. No plants were specifically avoided which suggests that chameleons were not particular about which plant species they perched on. However, the vegetation transects did not include areas avoided by the radio-tracked chameleons.

The radio-tracked chameleons avoided grazed grass, open sand and raised hills that were often dominated by large blombos (*Metalasia)* or sparse vegetation. Chameleons lose their cryptic and height advantage when on exposed ground and their lack of speed makes them especially vulnerable to predation. However,

occasionally chameleons moved short distance between vegetation separated by footpaths or low grass, but this was not directly observed. This suggests that chameleons are capable of moving across such areas, but minimise the time spent crossing these areas. This supports the suggestion that chameleons perch in denser vegetation cover to reduce risk of predation during the day. I doubt chameleons would risk crossing large open areas, especially if no suitable vegetation or potential mate visible across the area. The blombos provides suitable cover and perch height, as well as a wide selection of stem thicknesses and thus it remains unknown why chameleons avoid it.

Future improvements:

The area utilised, or sometimes home-range size, estimated by the minimum convex polygon (MCP) method appears to be the most commonly used method for reptiles (Cuadrado, 2006; Nicholson & Richards, 2011). It was chosen in this study for its simplicity and comparability to other studies; however, the calculation of the chameleon area of utilisation could have been improved by using a kernel method that allows concave area construction. The MCP method was unsuitable for one or two chameleons that underwent a rapid movement, resulting in an oversizing polygon created in-between the main areas utilised. Another method could have been devised to measure the distance travelled from a starting or average position and that directly measures the distance displaced over time.

Measuring the maximum vegetation height for perches of radio-tracked chameleon could have contributed to the models by accounting for variation introduced from the variable heights of plants. Radio-tracking a greater number of chameleons would have been preferable, as perch use could have been influenced by the surrounding vegetation, but funding and transmitter battery life constrained additional fieldwork. The 2014 night surveys of chameleon perch height and cover were done after the radio-tracking, but it would have been far better to record this for the radio-tracked chameleons during the tracking. Furthermore, measuring perch use and searching hourly for individuals could have altered their behaviour, and although they continued to forage and mate, we cannot completely discount this effect. We must remain careful when applying the findings from this study to other Cape dwarf chameleon populations on other sites owing to differences in population density, fragmentation severity or vegetation.

We found that smaller chameleons perched on thinner perches, which could have important consequences if this correlation to smaller, juvenile chameleons. A number of studies have suggested higher movement for smaller, younger chameleons (Butler, 2005; Tolley *et al.*, 2010). Thus juveniles could facilitate dispersal across transformed areas with thin stemmed grasses between habitat fragments and could yield valuable insights if investigated. This study could only speculate about the role predation plays in chameleon habitat selection and experimental studies are needed to further investigate this. Genetic analysis has been used in a number of studies to investigate the effects of fragmentation (Moore *et al.*, 2008; Louy *et al.*, 2007), including for the Cape dwarf chameleon in the Noordhoek Wetlands (Katz, Tolley & Bishop, 2013). However, to further assess the vulnerability of this species to fragmentation, genetic and tracking studies should now

focus on dispersal and geneflow between populations separated by a transformed matrix. Studies should be done before and after the creation of habitat corridors or new land transformation. In sub-urban environments, the effectiveness of fences and roads as dispersal barriers should also be investigated. Especially as the larger savanna flap-necked chameleon often crosses large roads (pers. obs.)

Conclusion

This study provides further evidence that the Cape dwarf chameleon is capable of migration between areas provided suitable vegetation links these habitats. Although males appear to compete for females and have a viewpoint advantage, they appear to move similar distances to females over a set duration. The risk of predation could explain the difference in day and night perch height and vegetation cover, implying that short or scattered vegetation with little cover could inhibit movement to other habitats. The ability of this species to disperse through vegetation could account for its presence and persistence in some of the highly transformed and fragmented gardens in Cape Town. Recent conservation strategies are targeting spatial processes to counteract the effects of habitat destruction and fragmentation (Huxel & Hastings, 1999), promoting conservation within and outside of protected areas (Mace, 2014). This study suggests that strategies such as vegetated corridors could successfully be implemented to encourage dispersal between habitat fragments and thus mitigate the effects of habitat fragmentation on the Cape dwarf chameleon.

REFERENCES

Abrahams, M. V & Dill, L.M. (1989) A Determination of the Energetic Equivalence of the Risk of Predation. *Ecology*. 70 (4), pp. 999–1007.

Aerts, P., Van Damme, R., Vanhooydonck, B., Zaaf, A. & Herrel, A. (2000) Lizard Locomotion: How Morphology Meets Ecology. *Netherlands Journal of Zoology*. 50 (2), pp. 261–277.

Aldridge, R.D. & Brown, W.S. (1995) Male Reproductive Cycle, Age at Maturity, and Cost of Reproduction in the Timber Rattlesnake (Crotalus horridus). *Journal of Herpetology*. 29 (3), pp. 399–407.

Anon (n.d.) *Working for Wetlands: Peninsula*. Available from: http://wetlands.sanbi.org/project_details.php?id=94 [Accessed 21 October 2014].

Avery, R.A., Bedford, J.D. & Newcombe, C.P. (1982) The Role of Thermoregulation in Lizard Biology: Predatory Efficiency in a Temperate Diurnal Basker. *Behavioral Ecology and Sociobiology*. 11 (4), pp. 261–267.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E. a (2011) Has the Earth's sixth mass extinction already arrived? *Nature*. 471 (7336), pp. 51–57.

Bivand, R., Keitt, T. & Rowlingson, B. (2013) *rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 0.8-14*. Available from: http://cran.r-project.org/package=rgdal.

Bleich, V.C., Bowyer, R.T. & Wehausen, J.D. (1997) Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs*. (134), pp. 3–50.

Bohrer, G., Nathan, R. & Volis, S. (2005) Effects of long-distance dispersal for metapopulation survival and genetic structure at ecological time and spatial scales. *Journal of Ecology*. 93 (5), pp. 1029–1040.

Branch, W.R. & Harrison, J.A. (2004) Conservation status and threats. In: William R Branch & James A Harrison (eds.). *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland*. SI/MAB Series #9. Smithsonian Institute, Washington, DC: pp. pp. 13–29.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology*. 58 (2), pp. 445–449.

Brown, K.S. & Brown, G.G. (1992) Habitat alteration and species loss in Brazilian forests. In: T C Whitmore & J A Sayer (eds.). *Tropical Deforestation and Species Extinction*. London: Chapman & Hall. pp. pp. 119–140.

Butler, M.A. (2005) Foraging mode of the chameleon , Bradypodion pumilum : a challenge to the sit-and-wait versus active forager paradigm ? *Biological Journal of the Linnean Society*. 84pp. 797–808.

Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*. 197pp. 516–519.

Carr, L.W. & Fahrig, L. (2001) Effect of Road Traffic on Two Amphibian Species of Differing Vagility. *Conservation Biology*. 15 (4), pp. 1071–1078.

Chiarello, A.G. (1999) Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. *Biological Conservation*. 89pp. 71–82.

Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, a. D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D. & Brotherton, P.N.M. (1999) Predation, group size and mortality in a cooperative mongoose, Suricata suricatta. *Journal of Animal Ecology*. 68 (4), pp. 672–683.

Cooper, W.E. (2000) Tradeoffs between Predation Risk and Feeding in a Lizard, the Broad-Headed Skink (Eumeces laticeps). *Behaviour*. 137 (9), pp. 1175–1189.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in ecology & evolution*. 14 (10), pp. 405–410.

Cuadrado, M. (1999) Body Colors Indicate the Reproductive Status of Female Common Chameleons: Experimental Evidence for the Intersex Communication Function. *Ethology*. 106pp. 79–91.

Cuadrado, M. (2006) Mate guarding and social mating system in male common chameleons (Chamaeleo chamaeleon). *Journal of Zoology*. 255 (4), pp. 425–435.

Cuadrado, M., Mawin, J., Lopez, P. & Martin, J. (2001) Camouflage and escape decisions in the common chameleon Chamaeleo chamaeleon. *Biological Journal of the Linnean Society*. 72pp. 547–554.

Eddy, W.F. (1977) A New Convex Hull Algorithm for Planar Sets. *ACM Transactions on Mathematical Software*. 3 (4), pp. 398–403.

Emlen, S.T. & Oring, L.W. (1977) Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science*. 197pp. 215–222.

Funk, W.C., Greene, A.E., Corn, P.S. & Allendorf, F.W. (2005) High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. *Biology letters*. 1 (1), pp. 13–16.

Garland, T. (1999) Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Behaviour*. 58pp. 77–83.

Herrel, A., Measey, G.J., Vanhooydonck, B. & Tolley, K. a. (2011) Functional consequences of morphological differentiation between populations of the Cape Dwarf Chameleon (Bradypodion pumilum). *Biological Journal of the Linnean Society*. 104 (3), pp. 692–700.

Holmes, P.M., Rebelo, A.G., Dorse, C. & Wood, J. (2012) Can Cape Town's unique biodiversity be saved? Balancing conservation imperatives and development needs. *Ecology and Society*. 17 (2), pp. 28.

Hopkins, K.P. & Tolley, K.A. (2011) Morphological variation in the Cape Dwarf Chameleon (Bradypodion pumilum) as a consequence of spatially explicit habitat structure differences. *Biological Journal of the Linnean Society*. 102pp. 878–888.

Huxel, G.R. & Hastings, A. (1999) Habitat Loss, Fragmentation, and Restoration. *Restoration Ecology*. 7 (3), pp. 309–315.

Jackson, J.C. (2007) *Reproduction in Dwarf Chameleons (Bradypodion) with particular reference to B. Pumilum occurring in fire-prone Fynbos habitat*. Stellenbosch University.

Katz, E.M. (2012) *Demographic and genetic variability in cape dwarf chameleons,*.

Katz, E.M., Tolley, K.A. & Altwegg, R. (2013) Survival and abundance of Cape dwarf chameleons, Bradypodion pumilum, inhabiting a transformed, semi-urban wetland. *Herpetological Journal*. 23pp. 179–186.

Katz, E.M., Tolley, K.A. & Bishop, J.M. (2013) Temporal changes in allelic variation among Cape Dwarf Chameleons, Bradypodion pumilum, inhabiting a transformed, semi-urban wetland. *African Journal of Herpetology*. 63 (1), pp. 1–12.

Keller, L.F. & Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends in ecology & evolution*. 17 (5), pp. 19–23.

Kotler, B.P. (1984) Risk of Predation and the Structure of Desert Rodent Communities. *Ecology*. 65 (3), pp. 689–701.

Lopez Ornat, A. & Greenberg, R. (1990) Sexual Segregation by Habitat in Migratory Warblers in Quintana Roo , Mexico. *The Auk*. 107 (3), pp. 539–543.

Louy, D., Habel, J.C., Schmitt, T., Assmann, T., Meyer, M. & Müller, P. (2007) Strongly diverging population genetic patterns of three skipper species: the role of habitat fragmentation and dispersal ability. *Conservation Genetics*. 8 (3), pp. 671–681.

Mace, G.M. (2014) Whose conservation? *Science*. 345 (6204), pp. 1558–1560.

Mace, G.M. & Harvey, P.H. (1983) Energetic constraints on home-range size. *The American Naturalist*. 121 (1), pp. 120–132.

Madsen, T. (1984) Movements, Home Range Size and Habitat Use of Radio-Tracked Grass Snakes (Natrix natrix) in Southern Sweden. *Copeia*. 1984 (3), pp. 707–713.

Madsen, T. & Shine, R. (1993) Temporal Variability in Sexual Selection Acting on Reproductive Tactics and Body Size in Male Snakes. *The American Naturalist*. 141 (1), pp. 167–171.

Maechler, B.D., Bolker, B. & S, W. (2014) *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7*. Available from: http://cran.r-project.org/package=lme4.

Mantyka-pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*. 18 (4), pp. 1239–1252.

Measey, G.J., Raselimanana, A. & Herrel, A. (2013) Ecology and Life History of Chameleons. In: Krystal A. Tolley & Anthony Herrel (eds.). *The Biology of Chameleons*. London: p. pp. 269.

Moore, J. a, Miller, H.C., Daugherty, C.H. & Nelson, N.J. (2008) Fine-scale genetic structure of a long-lived reptile reflects recent habitat modification. *Molecular ecology*. 17 (21), pp. 4630–4641.

Moore, J. & Ali, R. (1984) Are dispersal and inbreeding avoidance related? *Animal Behaviour*. 32 (1), pp. 94–112.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*. 403 (6772), pp. 853–858.

Nicholson, K.E. & Richards, P.M. (2011) Home-range size and overlap within an introduced population of the Cuban Knight Anole , Anolis equestris (Squamata : Iguanidae). *Phyllomedusa*. 10 (1), pp. 65–73.

Olsson, M. (1993) Male preference for large females and assortative mating for body size in the sand lizard (Lacerta agilis). *Behavioral Ecology*. 32 (5), pp. 337–341.

Pebesma, E.J. & Bivand, R.S. (2005) Classes and methods for spatial data in R. *R News*. 5 (2), .

Promislow, D.E.L., Montgomerie, R. & Martin, T.E. (1992) Mortality costs of sexual dimorphism in birds. *Proceedings: Biological Sciences*. 250 (1328), pp. 143–150.

Pusey, A. & Wolf, M. (1996) Inbreeding avoidance in animals. *Transactions in GIS*. 11 (5), pp. 201–206.

R Core Team (2013) *R: A Language and Environment for Statistical Computing R*.

Raimondo, D. & von Staden, L. (2009) Patterns and trends in the Red List of South African plants 2009. In: D Raimondo, L von Staden, W Foden, J E Victor, N A Helme, R C Turner, D A Kamundi, & P A Manyama (eds.). *Red List of South African Plants*. Pretoria: South African National Biodiversity Institute. p. pp. 668.

Rebelo, A.G., Boucher, C., Helme, N., Mucina, L. & Rutherford, M.C. (2006) Fynbos Biome. In: Ladislav Mucina & Michael C Rutherford (eds.). *The Vegetation of South Africa, Lesotho and Swaziland*. Pretoria: South African National Biodiversity Institute. p. pp. 807.

Rebelo, A.G., Holmes, P.M., Dorse, C. & Wood, J. (2011) Impacts of urbanization in a biodiversity hotspot: Conservation challenges in Metropolitan Cape Town. *South African Journal of Botany*. 77 (1), pp. 20–35.

Reed, D.H. & Frankham, R. (2003) Correlation between Fitness and Genetic Diversity. *Conservation Biology*. 17 (1), pp. 230–237.

Reinert, H.K. & Zappalorti, R.T. (1988) Timber Rattlesnakes (Crotalus horridus) of the Pine Barrens: Their Movement Patterns and Habitat Preference. *Copeia*. 1988 (4), pp. 964–978.

Roberts, A., Hockey, P.A.R., Dean, W.R.J. & Ryan, P. (2005) *Roberts' birds of southern Africa*. 7th edition. Cape Town: Trustees of the J. Voelcker Bird Book Fund.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological Consequences of Ecosystem Fragmentation: A Review. *Conservation Biology*. 5 (1), pp. 18–32.

Shaffer, M.L. (1981) Minimum for Species Population Sizes Conservation. *BioScience*. 31 (2), pp. 131–134.

Da Silva, J.M. & Tolley, K.A. (2013) Ecomorphological variation and sexual dimorphism in a recent radiation of dwarf chameleons (Bradypodion). *Biological Journal of the Linnean Society*. 109pp. 113–130.

Stuart-Fox, D.M., Moussalli, A., Marshall, N.J. & Owens, I.P.F. (2003) Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Animal Behaviour*. 66 (3), pp. 541–550.

Tolley, K. a., Chauke, L.F., Jackson, J.C. & Feldheim, K. a. (2014) Multiple paternity and sperm storage in the Cape Dwarf Chameleon (Bradypodion pumilum). *African Journal of Herpetology*. 63 (1), pp. 47–56.

Tolley, K.A. (2014) Family Chamaeleonidae. In: Michael F Bates, William R Branch, Aaron M Bauer, Marius Burger, Johan Marais, Graham Alexander, & Marienne de Villiers (eds.). *Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland*. 1st edition. Pretoria: Suricata. p. pp. 485.

Tolley, K.A. & Burger, M. (2007) *Chameleons of Southern Africa*. Cape Town: Struik Publishers.

Tolley, K.A., Raw, R.N. V, Altwegg, R. & Measey, G.J. (2010) Chameleons on the move : survival and movement of the Cape dwarf chameleon , Bradypodion pumilum , within a fragmented urban habitat. *African Zoology*. 45 (1), pp. 99–106.

Trivers, R.L. (1972) *Parental Investment and Sexual Selection*.

Vesakoski, O., Merilaita, S. & Jormalainen, V. (2008) Reckless males, rational females: dynamic trade-off between food and shelter in the marine isopod Idotea balthica. *Behavioural processes*. 79 (3), pp. 175–181.

Vitousek, P.M. (1997) Human Domination of Earth's Ecosystems. *Science*. 277 (5325), pp. 494–499.

Weckerly, F.W. (1998) Sexual segregation and competition in Roosevelt Elk. *Northwestern Naturalist*. 79 (3), pp. 113–118.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1988) Quantifying Threats to Imperiled Species in the United States. *BioScience*. 48 (8), pp. 607–615.

Yoder, J.M. (2004) The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology*. 15 (3), pp. 469–476.